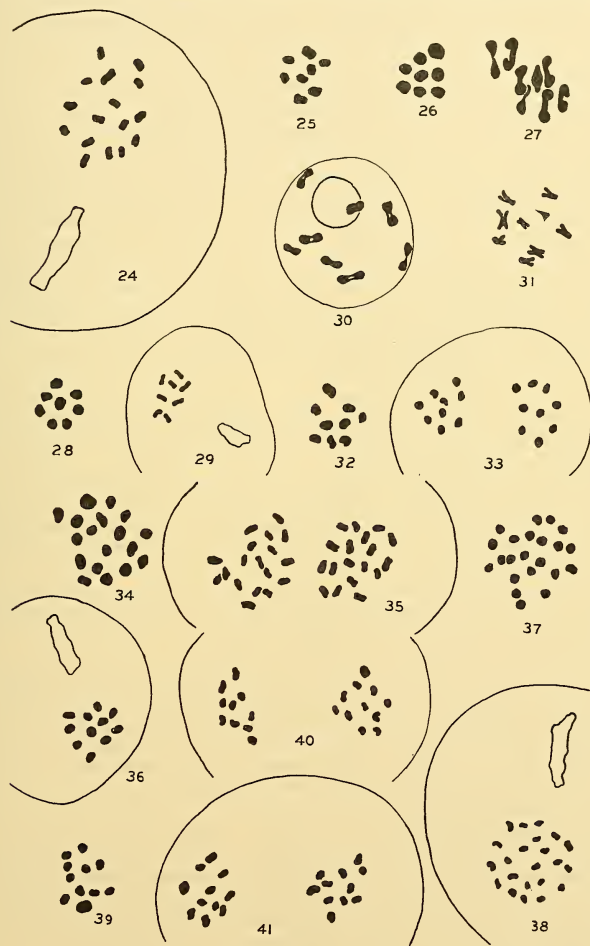


DISCUSSION.

Chromosome numbers in the *Euchamaelaucinae* have significance for the systematics of the subtribe, and have an important bearing on the interpretation of the phylogeny of the *Myrtaceae*, and its historical development in Australia.

The taxonomy of the Euchamaelaucinae.—In *Darwinia* ($n = 6, 7, 9$) and *Verticordia* ($n = 6, 8, 9, 11$) there is a similar pattern of variation in chromosome number, and



Text-figures 24-41.

24, *V. chrysanth*, 2-M. 25, *V. preissii*, 1-M. 26, *V. acerosa*, 1-M. 27, *V. acerosa*, early 1-A, side view. 28, *V. oxylepis*, 1-M. 29, *V. oxylepis*, 2-M. 30, *V. huegellii*, diakinesis. 31, *V. huegellii*, 2-M. 32, *V. insignis*, 1-M. 33, *V. insignis*, 2-M. 34, *V. habrantha*, 1-M. 35, *V. habrantha*, 2-M. 36, *V. picta*, 2-M. 37, *V. grandis*, 1-M. 38, *V. grandis*, 2-M. 39, *Pileanthus peduncularis*, 1-M. 40, *P. peduncularis*, 2-M. 41, *Chamaelaucium axillari*, 2-M. (All figures $\times 2000$.)

Homoranthus ($n = 9$) connects the two larger genera at the 9-chromosome level. Morphologically, *Darwinia* and *Verticordia* are distinguished by calycine characters. In the former, the five sepals are entire, but in the latter the sepals are deeply divided each into five plumose lobes, or into numerous hair-like parts. In *Homoranthus*, each sepal is produced into a single plumose bristle, or, in *H. darwinoides*, into five bristles. Both morphologically and cytologically, *Homoranthus* links the two larger genera. Benthams (1866) indicated that the genera of the Eucharmaelaucinae could be arranged in a linear morphological series as follows: *Actinodium*, *-Darwinia* § *Genetyllis*, *-Darwinia* § *Schaumannia*, *-Homoranthus*, *-Verticordia* § *Euverticordia*, *-Verticordia* § *Catocalyptra*, *-Chamaelaucium*.

On the basis of cytological and morphological evidence, two alternative views of the phyletic status of *Darwinia* and *Verticordia* may be proposed.

(a) The two genera, as at present established, are sound, and the chromosome number series present in each represent cases of parallel chromosomal evolution.

(b) The numerical patterns belong to the same series, and the phyletic status of the two genera is unsound. Parallel evolutionary development of calycine form in several lineages is required. A multiple origin of particular characters in a group involves no serious genetic difficulty, since various species must carry many homologous genes with similar mutational tendencies. The occurrence of similar mutations in different species of a genus is well known in *Drosophila*, *Triticum*, *Hordeum*, *Gossypium*, and in fact in almost every genus which has been investigated genetically. Such parallelisms provide the basis for the "Law of Homologous Variations" enunciated by Vavilov (1935). On the other hand, parallel series in chromosomal evolution have been demonstrated in *Crepis* (Babcock, 1949).

Choice between the two alternatives must await further cytological and systematic study, but the following suggestions are offered towards the revision of the group.

1. No taxonomic revision of *Darwinia* or *Verticordia* should be attempted without the incorporation of cytological data.

2. The 9-chromosome species in *Darwinia* should be separated from that genus, and perhaps combined with *Homoranthus*.

3. The genus *Verticordia*, as at present accepted, is a composite one and should be divided. The subdivision of the genus given by Benthams, however, is not likely to provide a satisfactory basis.

Verticordia grandiflora may be more akin to species of *Darwinia*, and the 11-chromosome species in *Verticordia* § *Catocalyptra* are allied to *Chamaelaucium*, and should be separated from other species of the present genus.

The phylogeny of the Myrtaceae.—Any consideration of the origin and evolution of the Myrtaceae must take into account the origin of the 11-chromosome genome which is generally characteristic of the family. The basic chromosome number in the Rosales, from which most systematists derive the Myrtales, is seven. Darlington and Mather (1949) consider that the primitive haploid number in the Angiosperms was seven, and Stebbins (1950) has suggested that many groups of woody Angiosperms with haploid numbers of 11, 13 and 19 have been derived from basic numbers of 6 or 7 by amphidiploidy and secondary polyploidy.

The basic number of 11 in the Myrtaceae is almost certainly a derived one, but any hypothesis on the evolutionary development of the family must depend on the status conceded to the 6-genome found in *Darwinia*. Three possibilities may be considered.

1. The 6-chromosome constitution in the Eucharmaelaucinae is primitive, and the 11-genome has arisen only once. This view would mean that the 11-chromosome species of the Eucharmaelaucinae, the Leptospermoideae and the Myrtoideae are all related at the 11-chromosome level. The view cannot reasonably be maintained.

2. The 6-chromosome genome is primitive, and the 11-chromosome genome has arisen on several or many occasions in different lineages. Independent origins in the Eucharmaelaucinae, in the other subtribes of the Chamaelaucaceae, in the Leptospermoideae, and in the Myrtoideae would be a minimum requirement. The method of origin would involve polyploidy to give a haploid number 12, followed by the loss of a chromosome

or of a centromere. This view would lead to an expectation of haploid numbers of 12 within the family, but Atchison's report (1947) of this number in some species of *Eucalyptus*, even if correct (Smith-White, 1948), is of no significance in this respect. It would indicate only a secondary derivation of 12 chromosomes from the 11-genom characteristic of *Eucalyptus*. The hypothesis does not take into account the intermediate haploid numbers of 7, 8 and 9 found in *Darwinia* and *Verticordia*, and must now be rejected.

3. The 11-chromosome genom is basic to the family, although having an earlier derivation from a lower number, and the chromosome complements of 6, 7, 8 and 9 found in the *Euchamaelaucinae* have arisen by reduction. Reducing series in chromosome numbers are not infrequent in many groups of Angiosperms (Darlington and Mather, 1949; Darlington and Janaki, 1944; Stebbins, 1950). Darlington (1937) has shown how such series arise from structural change and centromere loss. Tobgy (1943) has actually demonstrated this process in *Crepis*.

Hypothesis 3 is, consequently, much the most probable. On this basis, the chromosome number series in *Darwinia* and *Verticordia* represent either a single, or several parallel reducing series, $11 \rightarrow (10) \rightarrow 9 \rightarrow 8 \rightarrow 7 \rightarrow 6$, and the morphological series presented earlier should be read from right to left, i.e. from *Chamaelaucium* to *Actinodium*, and not in the opposite direction.

It follows, if this hypothesis is accepted, that the *Euchamaelaucinae* represent a group of genera which are both morphologically and cytologically specialized and derived. Andrews's view on the evolution of the Australian Myrtaceae receives confirmation rather than denial from the cytological evidence, and Atchison's conclusion that the cytological data support an ancient and monophyletic origin of the family is strengthened.

A new problem, however, arises. Why is it that, whereas chromosome constancy, with a low frequency of even such easy changes as polyploidy, has been a feature of the Myrtaceae, one small subtribe, with a relatively restricted distribution, has been able to undergo repeated steps in chromosome diminution? Perhaps the answer to this problem may be found in Darlington's suggestion (Darlington and Janaki, 1944) that liability to chromosomal alterations is dependent on the characteristics of chromosome architecture. The presence of heterochromatin close to the centromeres would perhaps allow a better chance of survival for individuals suffering centromere loss.

The historical development of the Euchamaelaucinae in Australia.—Crocker and Wood (1947) have suggested that the floras of eastern and western Australia have been isolated from each other practically continuously since the Miocene period. On the basis of cytological and geographical evidence and inference, it is possible to relate the development of the *Euchamaelaucinae* to this time scale.

The absence of vicarious species within genera, and the existence of vicarious genera such as the eastern *Homoranthus* and the western *Verticordia*, in the eastern and western regions suggest that considerable evolution at the species level has occurred since the development of the main intracontinental migration barrier. If slow rates of evolution are characteristic of woody Angiosperms (Stebbins, 1950), the migration barrier must be relatively ancient in origin, i.e. Miocene rather than Pleistocene, and the thesis of Crocker and Wood is supported. However, the 6-chromosome genom in *Darwinia* and the 9-chromosome genom in the *Darwinia-Homoranthus-Verticordia* complex are pan-Australian, and consequently their origins must have antedated this barrier, i.e. they must be placed in the early Miocene or in the Eocene. Early in the development of the *Euchamaelaucinae*, after the floristic isolation of Australia, and after their differentiation from the rest of the Myrtaceae, but before the floristic bisection of the continent, the subtribe must have suffered important changes in chromosome structure permitting the occurrence or survival of interchange and numerical diminution.

SUMMARY.

Additional chromosome number determinations are reported for the subtribe *Euchamaelaucinae* in the family Myrtaceae. Data are now available for 40 species, representing all genera and subgenera in the tribe.

The data demonstrate the existence of one or several reducing series in chromosome number within the subtribe, and especially in the larger genera *Darwinia* and *Verticordia*. These genera may prove to be unnatural groups, and there is need for their revision on a basis of both morphological and cytological evidence.

It is necessary to accept the Euchamaelaucinae as a cytologically specialized and derived group within the family. As a consequence, the author's earlier view of the phylogeny of the family is destroyed, and Andrews's conception is supported.

Acknowledgements.

This work was made possible by grants from the University Research Fund in 1950 and 1952, for study in Western Australia. Grateful acknowledgement is made to Dr. Brian Grieve and his staff, of the Botany Department, University of Western Australia, for the use of the facilities of that department. I am in debt to Mr. Stoate, Conservator of Forests, W.A., and to Mr. J. Harding, of the Forestry Department, for a great deal of assistance in field work. My thanks are also due to Miss E. Ashby, of Blackwood, South Australia, for access to her collection of Western Australian plants.

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A NEW SPECIES OF *HIBBERTIA* ANDR. FROM WESTERN AUSTRALIA.

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Department of Botany, University of Sydney.

(Plate i; four Text-figures.)

[Read 28th April, 1954.]

Synopsis.

A new species of the genus *Hibbertia* Andr. of the family Dilleniaceae from Western Australia is described.

The genus *Hibbertia* Andr., with about 140 species, is the largest of some 11 genera in the family Dilleniaceae. Hoogland (*Blumea*, 7, 1952, 1-145) places *Hibbertia* in the subfamily Dillenioidae. It is generally regarded as possessing some of the most primitive floral characters of that subfamily. Some species with completely actinomorphic flowers, with stamens ∞ and all fertile, and carpels ∞ , show this particularly well. The genus *Hibbertia* is known to occur in Madagascar, western and southern New Guinea, within the peripheral areas of Australia and in New Caledonia.

HIBBERTIA SERRATA, SP. NOV.

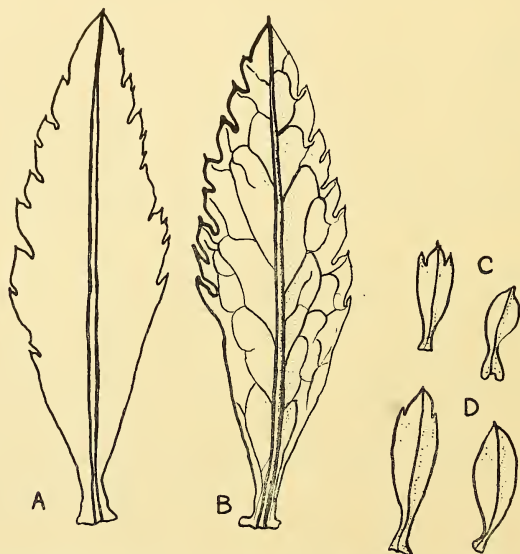
Type specimen: Pemberton, W.A., A. T. Hotchkiss, September 2, 1953; holotype in N.S.W. National Herbarium, isotypes in Sydney University Herbarium, Department of Agriculture Herbarium, Perth, Cornell University Herbarium.

Frutex erectus, pubescens, odoratus 1-1.5 m. altus; caules teretes; rami majores crassi et erecti; secundarii rami graciliores et ascendentes; cortex ramorum seniorum rubido-fuscus, pubescens, longitudine diffusus, denique particulis longis laxis disjunctis. Folia simplicia, exstipulata, alterna, sessilia, mollia, rhomboido-cuneata, leviter pubescentia infra, nervo medio et marginibus prope base villis simplicibus praecipue pubescentibus; margines plani; nervus medius subtus conspicuus et protusus; nervi secundarii angulum 45° nervo medio formantes; basis folii tumidula et leviter amplexans. Folia ramorum majorum 5-9 cm. longa \times 12-27 mm. lata, marginibus serrato-dentatis, apicibus mucronulatis; folia ramorum secundariorum 15-25 mm. longa \times 3-4 mm. lata, marginibus serratis vel integris. Inflorescentia brevis, arcta, axillaris; florum parvae, sessiliae, 2 (rare 3) bracteolis latis, fuscis, scariis, cuspidatis ca. 3.5 mm. longis \times 2.5 mm. latis, et 3 bracteis linearibus, foliaceis ca. 5-7 mm. longis; sepala 5, petala incurrentia; sepala ovata, acuminata 6-9 mm. longa \times 2.5-3 mm. lata, 3-nervata, pubescentia, imbricata, persistentia et fructos juvenes includentia; petala 5, late obovata, incisa, flava, caduca, 8 mm. longa \times 6 mm. lata; stamina ca. 20 (5-27), libera, ca. 4 mm. longa, circum gynoeceum in fasciculis cum carpellis alternantibus disposita; poris 2 obliquis subapicalibus; staminodia vel nulla vel ca. 3-6 (2-17), filiformes, clavata vel in forma semi-staminis, staminibus indefinite disposita. Carpella 2 vel 3, libera, ca. 5 mm. longa \times 2 mm. lata, glabrata, ovata, sessilia, folliculos maturitate formantia; stylus ca. 2.5 mm. longus, ab axe directus; stigma simplicissima; placentatio parietalis; ovuli 2; arillus albus, prope semen maturum tegens; semen globosum, laeve, fulgidum, rubido-fuscum, ca. 1.5 mm. diametro.

An erect pubescent, odorous shrub, 1-1.5 m. high; stems terete, the major branches coarse and erect, the secondary branches more slender and ascending; the bark on older branches reddish-brown, pubescent, splitting longitudinally and finally becoming loosened in long strips. Leaves simple, exstipulate, alternate, sessile, soft, slightly pubescent beneath with simple hairs especially on the midrib and on the margins near the base, rhomboid-cuneate to elliptical; margins flat; midrib prominent, protruding on the lower surface; secondary veins forming an angle of 45° with the midrib; base

of the leaf swollen and slightly stem-clasping. Leaves on major branches 5-9 cm. long \times 12-27 mm. broad, margins serrate-dentate, apices mucronulate; leaves on secondary branches 15-25 mm. long \times 3-4 mm. broad, margins serrate or entire.

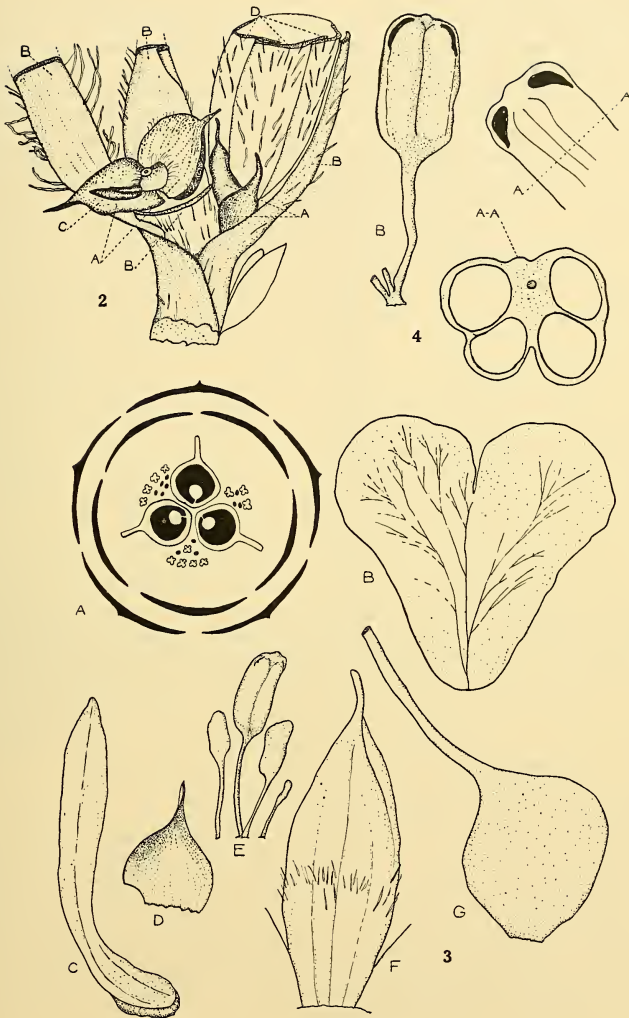
Flowers rather small, closely sessile, crowded in short axillary inflorescences; below each flower are 2 (3) small, brown, scarious, broad and cuspidate bracteoles about 3.5 mm. long \times 2.5 mm. broad; below which are 3 linear, foliaceous bracts about 5-7 mm. long; calyx of 5 sepals enclosing the petals; sepals ovate, acuminate, 6-9 mm. long \times 2.5-3 mm. broad, 3-nerved, pubescent, imbricate, persistent and closed again in the young fruit except for the scarious spreading tips; petals 5, broadly obovate, deeply notched, 8 mm. long \times 6 mm. broad, yellow, ephemeral; stamens about 20 (5-27), free,



Text-fig. 1.—*Hibbertia serrata*, sp. n. A, Large leaf from a major stem, natural size; B, Undersurface of same leaf showing venation; C, D, small leaves from a secondary branch, natural size.

about 4 mm. long, placed all round the gynoecium, usually in clusters alternating with the carpels; dehiscence of stamens subapical from 2 oblique pores opening from 4 chambers; staminodia either none or about 3-6 (2-17), filiform, clavate or half-stamen in size, placed indefinitely with the stamens. Carpels 2 or 3, free, about 5 mm. long \times 2 mm. broad, glabrous, ovate, sessile, ripening into a follicle; style about 2.5 mm. long, directed abaxially, stigma very simple; ovules two, attached to opposite sides of the adaxial placenta, usually only one maturing; arillus white, nearly covering the mature seed; seed spherical, smooth, shiny, reddish-brown, about 1.5 mm. in diameter.

The crushed leaves and stems have a peculiar odour suggestive of certain shrubs in the Compositae. The arrangement of the stamens at once places this species in the section *Cyclandra*. Large, flat, thin, pinnately-veined leaves with serrate margins are seldom found in this section (or the genus *Hibbertia*) outside the subsections *Hemihibbertiae* and *Bracteatae*. The possession of bracts and also staminodia are features common to both these groups, but the closely sessile condition of the flowers indicates a position in the *Bracteatae* for this species. Within this group it is allied to *H. montana*

Text-figs. 2-4. *Hibbertia serrata*, sp. n.

2.—A, Broad, brown bracts beneath the flower (flower removed); A', The same bracts beneath a flower bud; B, Linear foliaceous bracts; C, Bud arising above a bract; D, Sepals of flower bud.

3.—A, Diagram showing arrangement of floral parts, staminodia in solid black; B, Petal; C, Foliaceous bract; D, Broad, brown bract; E, A stamen with 3 staminodia; F, Sepal showing part of indumentum; G, Carpel.

4.—A-A, Transverse section through anther after anthesis; B, Stamen showing oblique, subapical pores.

Steud. and the closely related species *H. argentea* Steud., *H. pilosa* Steud., and *H. quadricolor* Domin, all of which differ from *H. montana* principally in the amount, type and position of their indumentum. *H. serrata* is quite different from the typical form of *H. montana* which has a low straggling habit with several stems; a conspicuous indumentum, especially on the sepals; small, thick, mostly entire leaves; and large flowers with large, conspicuous, shining, brown bracts. *H. montana* var. *major* Benth. (including *H. ovata* Steud. placed here by Bentham in *Fl. Aust.*) is described in *Fl. Aust.* as "Larger and more branched and often more or less hirsute, with long spreading hairs. Leaves usually larger, on luxuriant shoots often above 1½ or 2 in. long, broad and coarsely toothed, almost all less contracted at the base than in the normal form, and closely sessile. Some specimens of this variety look so different from *H. montana*, with their coarse habit, long spreading hairs, and broad-toothed leaves, that I at first retained them as a distinct species; but they pass into the smaller forms through so many intermediates, that I have been quite unable to draw any definite limits between them." Later authors have commented on this var. *major* and have perhaps enlarged the original concept of Bentham to include an increased amount of variation. Domin (1921-1922. *Vest. Kral. Ces. Spol.*) says "var. *major* Benth. . . . W.A.:—Yallingup and Cape Naturaliste, A. A. Dorrien-Smith. A very peculiar form entirely distinct from the typical *H. montana*. Its leaves are of very thin texture, on the upper surface glabrous and slightly hairy with scattered appressed hairs beneath, oblong-elliptical, the middle leaves about 8 cm long and almost 2.5 cm broad, very coarsely dentate. The scarios scales are broad but very short and fall off very early. The sepals are slightly hairy, the petals are large. Very near to our form are the specimens collected by Cecil Andrews (among granite rocks by Helena River, 17 m. east of Perth, 8 XI. 1902, W.A. Fl. First Coll. No. 14), which, however, are still more hairy and have somewhat smaller flowers. Hardly another *Hibbertia*-species could be found in which the indumentum, the size, form, dentation, texture of leaves, the size of the bracts and flowers would vary in such a degree; nevertheless Bentham is right in uniting all these forms, because there are transitions between them." It is of course impossible to say what Bentham would have done with these forms collected by Dorrien-Smith and Andrews. Bentham made no reference to the texture of the leaves, the size or falling of the bracts, or the size of the flowers in distinguishing var. *major* from the typical *H. montana*. Ostenfeld (*Dansk. Vidensk. Selskab.* 1921) also refers to specimens of var. *major* collected at Darlington (No. 302; 28 Aug. 1914, Cecil Andrews) and says: "This variety is very different from the true *H. montana*, and ought perhaps be taken as a separate species." He gives no description of the specimens.

About half the flowers examined contained no staminodia but in other flowers from the same plant staminodia were numerous and occasionally exceeded the stamens in numbers. The staminodia have no definite position being placed usually outside the stamens but occasionally among or inside the stamens. The significance of staminodia in this group is uncertain. Bentham in *Fl. Aust.* records staminodia in no species of the Bracteatae except *H. mylnei*. Domin records staminodia in *H. quadricolor* Domin. The presence of staminodia in some species of the Bracteatae may illustrate a transitional tendency between the Bracteatae and the Hemihibbertiae where staminodia are always present. The presence of staminodia in *H. serrata* is correlated with the number of carpels as seen in the accompanying table.

I have concluded that *H. serrata* should be erected as a new species very distinct from *H. montana* and its allies. *H. montana* var. *major* is intermediate in some characters but does not approach *H. serrata* as closely as it does to *H. montana* with which it appears to intergrade. *H. serrata* would include the tall robust forms which have thin, coarsely serrate leaves, short inconspicuous bracts, smaller flowers and more or less indumentum. It is probable that the specimens of Dorrien-Smith and Andrews, cited by Domin whose description indicates that they have thin leaves and differ in only minor ways from the type of *H. serrata*, also belong to this new species.